J. Physiol. (1976), **256**, *pp.* 573–600
With 2 plates and 13 text-figures
Printed in Great Britain

RECEPTIVE FIELDS OF UNMYELINATED VENTRAL ROOT AFFERENT FIBRES IN THE CAT

By G. L. CLIFTON, R. E. COGGESHALL, W. H. VANCE AND W. D. WILLIS

From the Departments of Anatomy and of Physiology and Biophysics and the Marine Biomedical Institute, the University of Texas Medical Branch, Galveston, Texas 77550, U.S.A.

(*Received 2 July 1975*)

SUMMARY

1. The receptive fields were determined for 118 afferent fibres in the S2, S3 and Ca (caudal) 1 ventral roots of the cat. Of these fibres, ninety-three were unmyelinated, another eleven were probably unmyelinated, and fourteen were myelinated, according to estimates of their conduction velocities.

2. Confirmation that the recordings were from ventral root filaments came from electron microscopic inspection of ten of the filaments from which recordings of the activity of unmyelinated afferents were made.

3. Receptive fields were demonstrated for twelve unmyelinated afferent fibres in the distal stumps of the S2 and S3 ventral roots which had been sectioned 3 weeks previously, indicating that the cell bodies giving rise to these fibres were not in the spinal cord.

4. The action potentials of some of the unmyelinated ventral root afferent fibres were complex, suggesting branching of the afferents within the ventral root.

5. One third of the unmyelinated ventral root afferents had receptive fields in somatic structures: the skin and deep tissues.

6. Two thirds of the unmyelinated ventral root afferents had receptive fields in the viscera of the pelvis: the bladder, urethra, vagina, and lower bowel.

7. Many of the unmyelinated afferents in the ventral roots, especially those with cutaneous receptive fields, had high thresholds and may participate in nociception.

8. It is concluded that the cat ventral root contains a major sensory component and that the Law of Bell and Magendie is not an accurate description of the organization of the ventral root in this animal.

INTRODUCTION

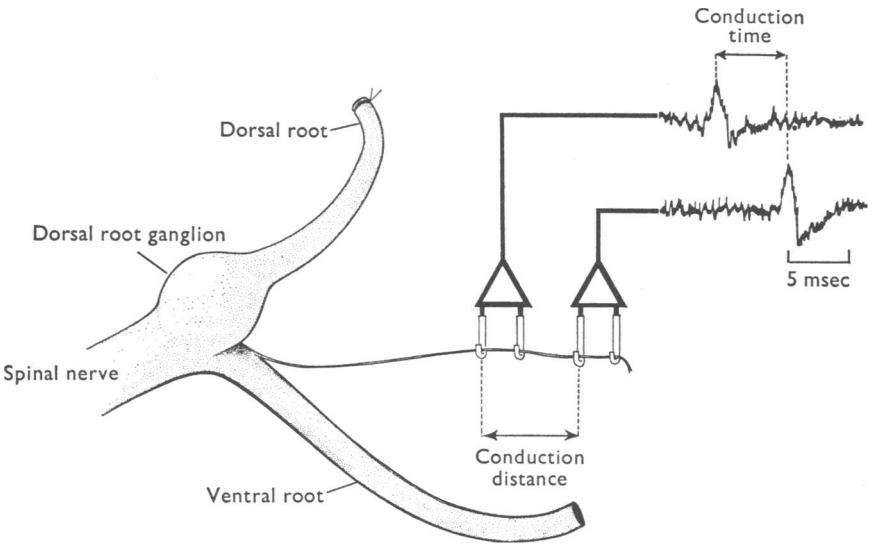
The validity of the Law of Bell and Magendie concerning the separation of function of the spinal roots has been accepted since the early 1800s (Bell, 1811; Magendie, 1822*a*; Cranefield, 1974). However, there have always been observations that are difficult to reconcile with this generalization. For example, (1) experimental and clinical investigations have reported various sensory phenomena when the ventral roots are manipulated (Magendie, 1822*b*; Bernard, 1858; Kidd, 1911; Lehmann, 1924; Wartenberg, 1928; Shaw, 1933; Frykholm, Hyde, Norlen & Skoglund, 1953; White & Sweet, 1955); (2) dorsal rhizotomy often fails to relieve chronic pain (White & Sweet, 1955; Loeser, 1974; Onofrio, 1974); and (3) morphological (Sherrington, 1894; Windle, 1931; Dimsdale & Kemp, 1966; Webber & Wemett, 1966; Mikeladze, 1965) and physiological (Dimsdale & Kemp, 1966; Kato & Hirata, 1968; Ryall & Piercey, 1970; Kato & Tanji, 1971) studies show that there are myelinated afferent fibres in the ventral root. However, the clinical data are not usually accepted as demonstrating that there is an important sensory component in the ventral root (Davis & Pollock, 1930; White & Sweet, 1955), and the number of myelinated afferent fibres seems to be small and variable (Sherrington, 1894; Windle, 1931). Thus, there has been no generally perceived need to modify the Law of Bell and Magendie.

Recently, however, there have been reports indicating that the number of sensory fibres, at least in certain cat ventral roots, has been seriously underestimated (Coggeshall, Coulter & Willis, 1974). As demonstrated in the companion paper to the present study (Applebaum, Clifton, Coggeshall, Coulter, Vance & Willis, 1975), approximately 29% of the fibres in the cat S3 and Ca 1 ventral roots are unmyelinated and half of these arise from dorsal root ganglion cells. The presumption is that the ventral root axons arising from these dorsal root ganglion cells are sensory. To provide evidence that this is the case, it would be desirable to demonstrate peripheral receptive fields of ventral root unmyelinated fibres. The present study is an investigation of receptive fields in somatic and visceral structures innervated by ventral root unmyelinated fibres at the S3 and Ca 1 segmental levels. The conclusion is that the ventral roots at these levels contain a substantial sensory component, and therefore we feel that the Law of Bell and Magendie is not an accurate description of the organization of the ventral spinal roots of the cat.

Preliminary reports of some of this work have previously been published (Clifton, Vance, Applebaum, Coggeshall & Willis, 1974; Coggeshall, Clifton, Vance & Applebaum, 1975; Vance, Clifton, Coggeshall & Willis, 1975).

METHODS

Experiments were performed on thirty-one adult cats weighing 2·5–5·0 kg. Anaesthesia was induced with halothane and nitrous oxide mixed with oxygen and maintained with α-chloralose (80 mg/kg I.V.). The animals were immobilized with gallamine triethiodide and ventilated artificially. A laminectomy was done to expose the lumbosacral enlargement of the spinal cord. A latex balloon was inserted into the urinary bladder through incisions in the left flank and bladder wall; the incisions were closed around a plastic tube secured to the neck of the balloon. Another balloon was inserted into the rectum or distal colon. Water could be injected to distend either balloon, and the pressure was monitored with a pressure transducer. The animal was attached to a rigid metal frame by clamps on the L4 vertebra and the iliac crests. The spinal cord was covered by a pool of warmed paraffin oil, and body temperature was maintained near 37° C.



Text-fig. 1. Recording arrangement. A filament of the ventral root is shown lying across two pairs of recording electrodes. The specimen records show the diphasic action potential of an unmyelinated ventral root afferent fibre propagating successively past the distal and then the proximal pairs of electrodes. The conduction velocity (1·0 m/sec) was determined from the conduction distance (6 mm) and the conduction time (6 msec, measured peak-to-peak).

After the dura was incised, the S3 and Ca 1 spinal roots were identified. The dorsal root on one side at S3 was traced to its entrance into the spinal cord, tied, cut, and reflected back to the dura (Text-fig. 1). The corresponding ventral root was severed near the spinal cord. A pair of stimulating electrodes was often placed beneath the ventral root adjacent to its exit through the dura. With the aid of a dissecting microscope, thin filaments were teased from the ventral root with fine forceps. Each filament in turn was placed across two pairs of recording electrodes (Text-fig. 1). The electrodes of each pair were separated by a fixed distance of 2 mm, while the

distal electrodes of the two pairs were separated by 6 mm. Activity recorded from each pair of electrodes was led to a differential amplifier; the activity was displayed simultaneously on two traces of a split beam oscilloscope. A permanent record was made on 35 mm film. When a unitary action potential of sufficient amplitude was observed, it could be used to trigger a window discriminator pulse, which was recorded on a pen writer. In some animals, after the activity of a filament was investigated, the filament was removed and fixed by immersion for electron microscopy. Filaments of comparable size were removed from dorsal roots at the same level in control animals. The fixative, preparative techniques, and electron microscopic examinations were as described in the preceding paper (Applebaum *et al.* 1975). Recording continued until the ventral root was completely subdivided, and then the same procedure was repeated for the Ca 1 ventral root on the same side and for the S3 and Ca 1 ventral roots on the contralateral side. In one animal, the S2 ventral root was employed.

The activity of single units conducting towards the spinal cord was sought in the recordings. The activity was sometimes spontaneous, but often it had to be evoked by stimulation of structures within the pelvis, the perineal skin, or the tail. In some experiments, activity was evoked by electrical stimulation of the ventral root near its exit through the dura, but it was usually not necessary to do this. In cases where electrical stimulation was necessary, conduction velocity was determined by the latency of the action potential and the conduction distance from the cathode to the recording electrode. In these units identification of the receptive field was by the demonstration that the action potential elicited by stimulation of the receptive field blocked the action potential evoked by electrical stimulation (Paintal, 1953; Clifton *et al.* 1974). In most cases, however, conduction velocity was determined from the delay in conduction between the two pairs of recording electrodes (Text-fig. 1). Identification of the action potentials of a single unit in such cases depended upon observation of a characteristic wave form and a consistent delay between the spikes recorded from the two sets of electrodes. The activity was considered to be from a ventral root afferent fibre if it conducted toward the spinal cord (i.e. the action potential was recorded successively by the distal and then the proximal electrode pairs) and/or if a receptive field could be demonstrated. The afferent fibre was considered to be unmyelinated if its conduction velocity was less than 2·5 m/sec (Gasser, 1950).

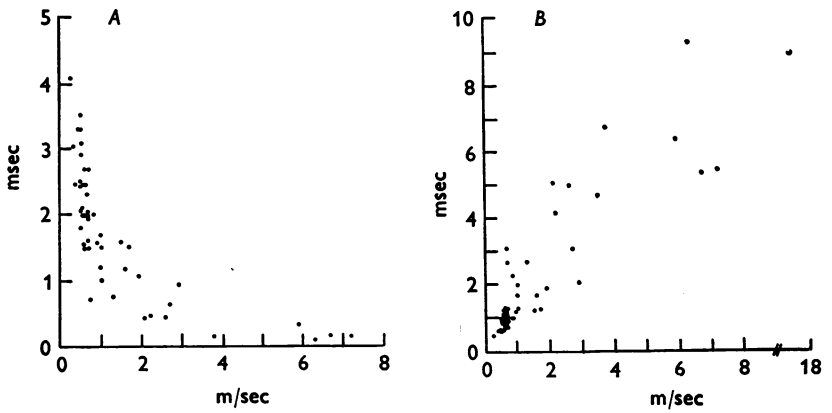
RESULTS

Identification of unmyelinated ventral root afferents

The activity of 106 single units was recorded from ventral roots at the S3 and Ca 1 segmental levels in thirty animals and of twelve units from chronically sectioned S2 and S3 ventral roots in one animal. Of these units, ninety-three were considered to be unmyelinated sensory fibres, since they had conduction velocities of less than 2·5 m/sec and demonstrable receptive fields. The conduction velocities of eleven units could not be measured directly, because the spike was recorded from only one of the pairs of electrodes and the refractory test was not used. In these cases, an estimate of conduction velocity was obtained from the spike duration (see below, Text-fig. 2). Although these units were probably unmyelinated, this characterization is tentative. In any case, these units were ventral root

afferents, since their receptive fields could be demonstrated. The receptive fields of fourteen myelinated ventral root afferents were also studied.

To estimate conduction velocity when the action potential was recorded by only one pair of electrodes, an effort was made to correlate conduction velocity with a parameter of the action potential. Total duration and peak–peak time were calculated from spikes of units of known conduction velocities. These units had conduction velocities characteristic of both myelinated and unmyelinated axons. The conduction velocities were calculated, as described in the Methods section, by the delay in conduction between two electrode pairs. Statistical analysis showed peak–peak time to have the best correlation with conduction velocity. Text-fig. 2*A* shows



Text-fig. 2. Relationship between spike duration and conduction velocity. In *A*, the peak–peak durations of the diphasic action potentials of forty unmyelinated and nine myelinated ventral root afferent fibres are plotted against conduction velocity determined by the method illustrated in Text-fig. 1. For *B*, the conduction velocities of the same fibres, plus one additional myelinated axon, were determined in two ways. The values plotted along the abscissa are the same as in *A*, while those along the ordinate are calculated by using the distance between the electrodes of a single pair (2 mm) as the conduction distance and the peak–peak action potential duration as the conduction time, on the assumption that each peak represents the arrival time of the action potential at one of the electrodes.

a plot of conduction velocity against peak–peak spike durations for fifty units. Text-fig. 2*B* is conduction velocity calculated in the usual way plotted against conduction velocity based on the assumption that the initial peak of the action potential represents the arrival of the spike at one electrode while the second peak indicates the arrival of the spike at the second electrode of the pair, giving a conduction delay for a distance of 2 mm. Using this method, eleven units which could be recorded from one

electrode pair had spikes with peak–peak times greater than 1 msec and thus were probably unmyelinated. However, the designation as unmyelinated is tentative (cf. Paintal, 1967). One difficulty is that the peak–peak spike duration in any given instance might be altered by a conduction block.

Care was taken to distinguish the dorsal from the ventral root before the ventral root was fasciculated for recording. The spontaneous activity recorded from ventral root filaments was less than that recorded from dorsal root filaments, which could be recognized by the presence of many spontaneously discharging myelinated units. Furthermore, we examined

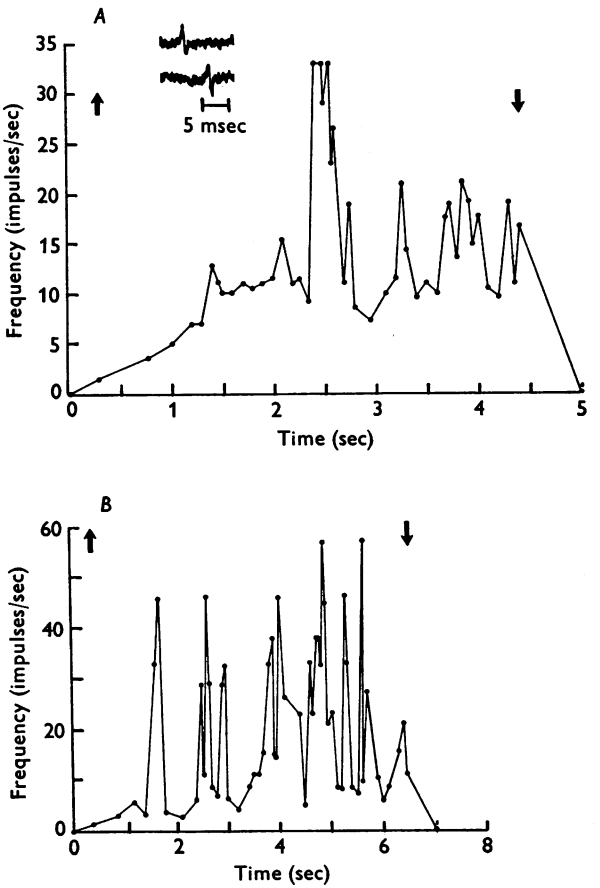
TABLE 1. Number of myelinated and unmyelinated axons in filaments of the dorsal and ventral roots

Dorsal root					Ventral root				
Filament no.	Myelinated fibres	%	Unmyelinated fibres	%	Filament no.	Myelinated fibres	%	Unmyelinated fibres	%
DR 1	90	57	69	43	VR 1	109	74	39	26
DR 2	196	35	370	65	VR 2	81	84	15	16
DR 3	87	62	54	38	VR 3	83	92	7	8
DR 4	85	44	107	56	VR 4	56	73	21	27
DR 5	33	42	46	58	VR 5	69	83	14	17
					VR 6	65	64	37	36
Total	491	—	646	—	VR 7	36	68	17	32
Average	98	43	129	57	VR 8	57	70	24	30
					VR 9	47	87	7	13
					VR 10	51	74	18	26
					Total	609	—	198	—
					Average	61	76	20	24

in the electron microscope ten filaments from which afferent activity in unmyelinated fibres had been recorded. A section of one of the filaments is shown at low and high magnification in Pl. 1. Counts were made of the numbers of unmyelinated and myelinated fibres in each of the ventral root filaments and also in five dorsal root filaments from the same segmental levels. The fibre counts are given in Table 1. It can be seen that the ventral root filaments contained an average of twenty unmyelinated and sixty-one myelinated fibres, with the unmyelinated fibres representing 24% of the total. This is close to the figure of 29% for the counts of the S3 and Ca1 ventral roots reported in the preceding paper (Applebaum *et al.* 1975). By contrast, the dorsal root filaments were clearly different and composed of 57% unmyelinated and 43% myelinated fibres.

Text-fig. 3*A* shows the activity of an unmyelinated ventral root afferent fibre recorded from the ventral root filament illustrated in Pl. 1. The inset

is the action potential of the unit, while the graph shows an increase in the instantaneous frequency of firing of the unit produced by stimulation of its receptive field. The effective stimulus was pressure applied to perianal tissue.



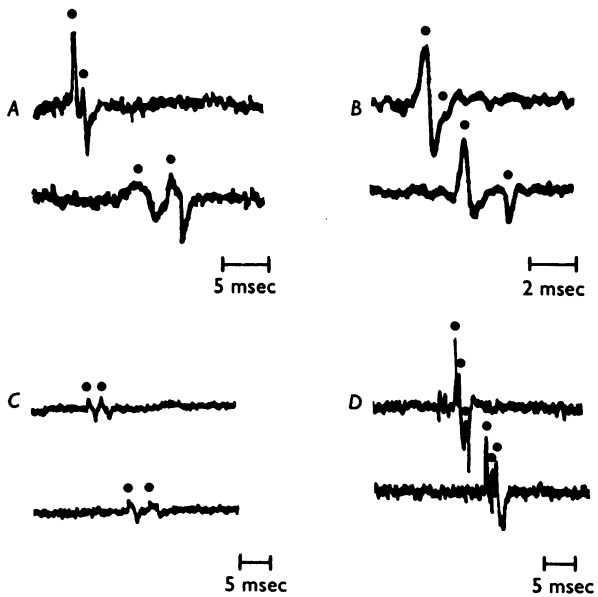
Text-fig. 3. Activity of unmyelinated ventral root afferents. In *A* is shown a plot of the instantaneous frequency of an unmyelinated afferent fibre (conduction velocity of 1·2 msec) in response to the application of pressure to perianal tissue. The onset of the stimulus is indicated by the first arrow, while the termination of the pressure is shown by the second arrow. The instantaneous frequency was determined from interspike intervals measured on a continuous film strip recording. The action potential of the unit is shown in the inset. The unit was recorded from the ventral root filament shown in the electron micrograph in Pl. 1. In *B* is shown an instantaneous frequency plot of the response of an unmyelinated afferent (conduction velocity of 1·2 m/sec) recorded from a filament of the distal stump of a ventral root which had been sectioned three weeks previously. The stimulus was pinching the rectal mucosa with a fine forceps.

Another possible concern was that direct mechanical stimulation of peripheral axons might activate ventral root efferents antidromically and that such activity might be misinterpreted as afferent. This possibility seemed remote, since unmyelinated efferent axons are not known to project from the spinal cord directly to peripheral target organs. Nevertheless, to confirm that unmyelinated ventral root afferents could be demonstrated in the absence of functional efferent fibres, we examined an animal in which the S2 and S3 ventral roots had been sectioned near the spinal cord 3 weeks before the experiment. Several millimetres of ventral root were removed at the time of surgery to prevent reapposition of the severed stumps. The activity of twelve unmyelinated afferent fibres were recorded in this animal. Eight of the units were in the S2 ventral root, while four were in the S3 ventral root. The receptive fields of the S2 ventral root afferents were all cutaneous, whereas the receptive fields of the S3 afferents were in visceral structures and were similar to our other units. Pl. 2 shows electron microscopic views at low and high magnification of one filament from the S3 ventral root of this animal. The degeneration of myelinated fibres is obvious, thus demonstrating that the root was cut. The presence of intact unmyelinated axons is also apparent, confirming that the cell bodies of the myelinated axons were located proximal to the cut and the cell bodies of at least some of the unmyelinated axons were located distal to the cut. The activity of a ventral root unmyelinated afferent in a distal stump of a sectioned ventral root is shown in Text-fig. 3*B*. The receptive field was in the rectal mucosa, and the graph shows the elevation in instantaneous frequency of discharge of the unit in response to pinching the mucosa.

Action potential wave forms

Most of the action potentials of unmyelinated afferent fibres recorded from ventral root filaments had simple diphasic wave forms (e.g. those shown in Text-fig. 1). However, in twelve instances the wave forms of the action potentials recorded from both pairs of electrodes were complex (e.g. Text-figs. 4 and 7). In most cases, these complex potentials could be interpreted as two diphasic spikes (Text-fig. 4*A–C*). The first spike had a faster conduction velocity than the second, suggesting that the records were from two different diameter branches of the same axon. In one instance (Text-fig. 4*B*), the conduction velocity of one branch was in the range for myelinated fibres (3·9 m/sec). The activity was assumed to be from a single neurone in each case, since both spikes occurred with the same time relationships whenever the cell discharged. In one instance, the action potential seemed to be composed of three components (Text-fig. 4*D*). An additional nine units had complex action potentials at one pair of elec-

trodes but a simple action potential at the other pair. It is possible that these were also afferents which bifurcated within the ventral root, but that conduction in one of the branches was blocked between the electrode pairs. Thus, 13–23 % of the unmyelinated ventral root afferents studied probably had two or more branches in the ventral root. A disproportionate number of these fibres were in the animal which had had a chronic ventral root section (three of the twelve units with complex spikes recorded by both



Text-fig. 4. Complex wave forms. Some of the ventral root afferent fibres had complex action potentials. The components of several of these are indicated by the dots in *A–D*. The pairs of records in *A–C* show that the action potentials at the distal electrode pair are closer together in time (upper traces) than those at the proximal electrode pair (lower traces), suggesting that the records are from two branches of an afferent axon having different conduction velocities. On this assumption, the conduction velocities would be: 0·9 and 0·6 m/sec for *A*; 3·9 and 2·1 m/sec for *B*; and 1·0 and 0·8 m/sec for *C*. The unit in *D* appears to have a triple spike, suggesting three branches, all of which conducted at about 1·2 m/sec.

sets of electrodes and two of the nine units in which complex spikes were seen only at one pair of electrodes). It is possible that the branching in this animal was in part due to sprouting of several afferent axons. Nevertheless, the frequency of complex spikes in the other animals suggests that between 11 and 20 % of ventral root unmyelinated afferents branch within the ventral root before reaching the spinal cord.

Receptive field locations

The locations of the receptive fields of ninety-three unmyelinated afferents and of eleven other afferents which may have been unmyelinated (based on their peak–peak spike durations) are listed in Table 2. It is likely that structures other than those listed were innervated by unmyelinated ventral root afferents, since many structures could not be effectively stimulated. Most of the structures listed were stimulated in most of the animals. In addition, the mesentery and parts of the colon were stimulated in thirteen animals through an abdominal incision.

TABLE 2. Locations of receptive fields of unmyelinated ventral root afferents

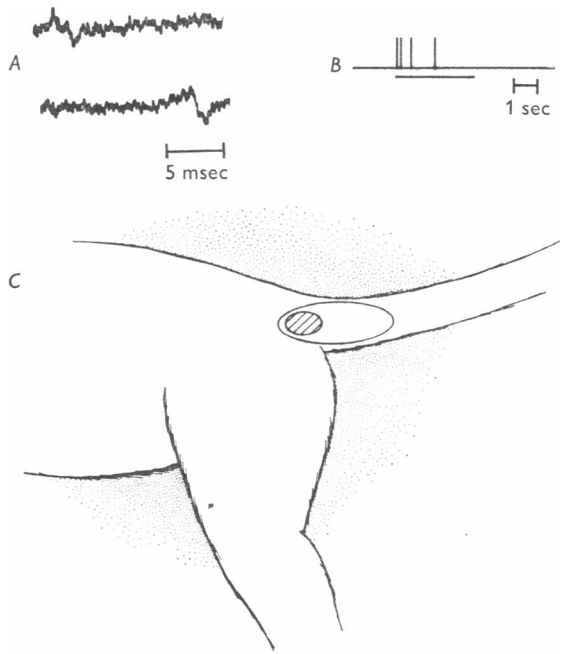
Location of receptive field	Number of unmyelinated afferents	Number of afferents which were probably unmyelinated	% of total
Somatic			
Cutaneous	21	3	23
Deep	9	1	10
	30	4	33
Visceral:			
Bladder	11	0	10
Urethra, vagina and penis	14	2	15
Gut mucosal	24	4	27
Gut distension	14	1	14
	63	7	67
Total	93	11	100

As indicated in Table 2, somatic afferents were found which innervated the skin and deep receptors. Most of the afferents supplied visceral structures such as lower bowel mucosa as well as the genito-urinary tract, including the bladder, vagina and urethra. The fourteen myelinated afferents supplied a comparable variety of structures.

Somatic receptive fields

Cutaneous. A total of twenty-eight cutaneous receptors were characterized. Of these, twenty-one had axons which conducted at a velocity appropriate to unmyelinated fibres, while an additional three units were probably unmyelinated because their peak–peak spike durations were greater than 1 msec. Four units had conduction velocities characteristic of small myelinated fibres, greater than 2·5 m/sec. These units were generally of high threshold. Of the twenty units examined with von Frey filaments, two could not be activated at all, four required filaments which bent at forces of 100 g or above, while only three had thresholds less than 5 g. Eleven units had von Frey thresholds between 5 and 20 g.

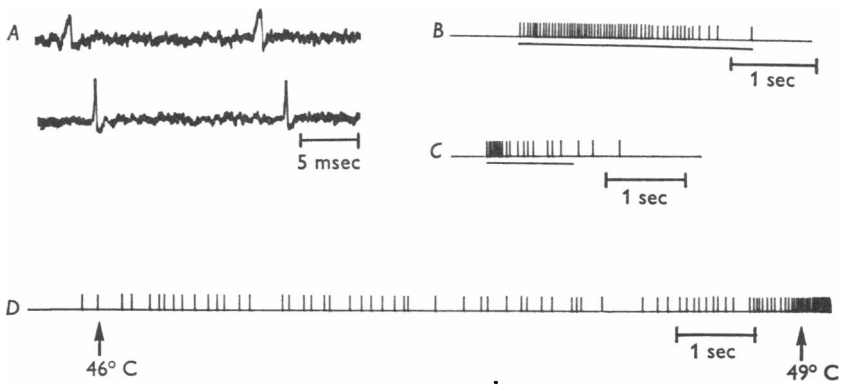
Some of the properties of typical units are illustrated in Text-figs. 5 and 6. Text-fig. 5*A* shows the action potentials of one unit and 5*B* is the window discriminator output in response to activation of the receptor by an 8·5 g von Frey filament. The location of the receptive field is shown in 5*C*. Characteristically, the cutaneous units had receptive fields around the base of the tail, perianal skin, genitalia or on the dorsum of the thigh.



Text-fig. 5. High threshold mechanoreceptor. The action potential of a ventral root unmyelinated afferent is shown in *A*; the conduction velocity was 0·5 m/sec. The action potential was used to trigger window discriminator pulses, which were then recorded on a pen-writer, as seen in *B*. The response in *B* was to the application of a von Frey filament to the receptive field, which was on the skin in the area shown in *C*. The receptive field had a zone of maximum sensitivity, shown by the shaded region in the drawing, and a broader area of less sensitivity, shown by the unshaded part of the oval. The threshold of the unit in the most sensitive part of the receptive field was 8·5 g, using graded von Frey filaments. There were no responses to thermal or chemical stimuli, and so the unit was classified as a high threshold mechanoreceptor.

Most of the units had receptive field areas of 2 or 3 cm^2, with a several mm^2 central area of maximum sensitivity. The shaded area in Text-fig. 5*C* outlines such an area of maximum sensitivity. This unit was classified as a high threshold mechanoreceptor.

Three of the units were polymodal nociceptors (Bessou & Perl, 1969). These units gave strong responses to heat, noxious pinch and irritant chemicals, and weak responses to cold. Text-fig. 6 illustrates the responses of such a unit. The action potential is shown in *A*. The response in *B* is to the application of a small arterial clamp to the skin. *C* shows the result of application of a test-tube filled with water at 4° C to the skin and *D* to progressive heating of the skin with a thermal probe (Steadman, 1968). The times at which the probe reached temperatures of 46 and 49° C are marked by arrows; note that the threshold was near 46° C and that the discharge frequency increased substantially at 49° C.

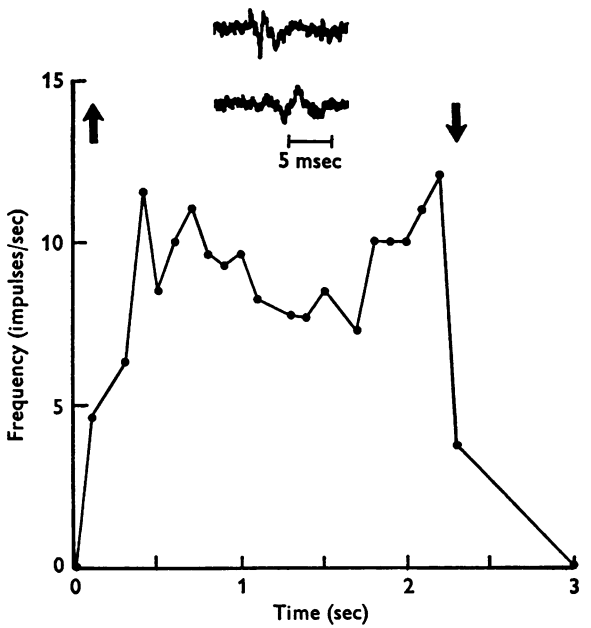


Text-fig. 6. Polymodal nociceptor. Two successive action potentials of a ventral root afferent conducting at 2·1 m/sec are shown in *A*; although the wave form of the spike at the distal electrode pair was slower than that at the proximal electrodes, the two events were always time-locked. Window discriminator pulses in *B–D* show the responses of the unit to the following cutaneous stimuli; *B*, attachment of a small arterial clip (a noxious mechanical stimulus); *C*, application of a test-tube containing water at 4° C; and *D*, noxious heating. The mechanical stimuli associated with contacting the skin with a test-tube or the thermal probe did not themselves activate the unit. In *D*, the temperature of the thermal probe was rising throughout the record, attaining 46 and 49° C at approximately the times indicated.

The cutaneous receptive fields of four myelinated fibres were characterized. These units did not respond to heat, cold or chemical irritants, but they did respond to application of arterial clips to the skin. Thresholds of 2·05 and 3·7 g were found for the two units examined with von Frey hairs.

Deep somatic. Receptive fields in deep somatic structures were observed on eleven occasions. Conduction velocities appropriate for unmyelinated fibres were found in nine instances, and a conduction velocity below 2·5 m/sec was estimated for one unit. Four of these units responded to

bending of the tail at a specific joint and could therefore be considered proprioceptors. However, the intensity of the stimulus may have approached a nociceptive level. A myelinated fibre was also found which could be activated by bending the tail. One unmyelinated unit, with a receptive field located in the left anal skin fold, responded to gross movements of the perirectal tissue. In no case did heat, cold, pinch, irritant chemicals or von Frey filaments applied to the skin activate the units with 'deep' receptive fields.

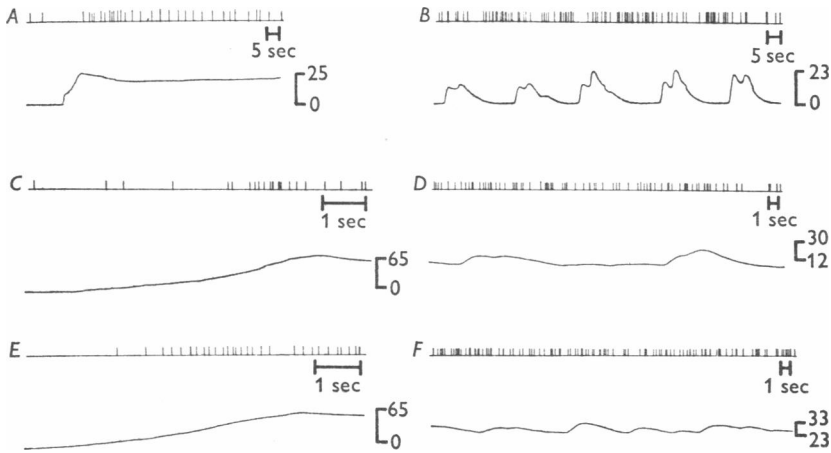


Text-fig. 7. Unit responding to bending tail. The instantaneous frequency is shown of the discharge of a unit in response to flexion of the tail at the joint between the sixth and seventh caudal vertebrae. The joint was flexed at the time indicated by the first arrow, and it was returned to its normal position at the second arrow. The complex action potential of the unit is shown in the inset. The conduction velocities of the two components of the spike were 1·1 and 0·8 msec.

Text-fig. 7 shows the action potential of one such unit and an instantaneous frequency plot of the unit's activity following flexion of the tail at the joint between the 6th and 7th caudal vertebrae. The first arrow marks the onset of flexion, while the second arrow marks the return of the joint to its normal position.

Genito-urinary

Bladder. A total of seventeen units had receptive fields in the bladder. Of these, eleven were shown to be unmyelinated by their conduction velocities, four units were myelinated on the basis of their peak–peak duration and an additional two units were estimated to be myelinated on the basis of the action potential duration.

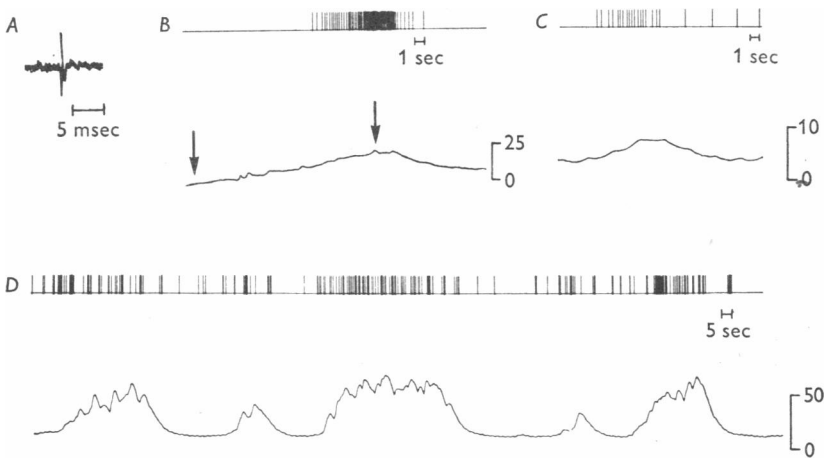


Text-fig. 8. Unmyelinated afferents supplying the bladder. The responses of three different unmyelinated afferent fibres are shown by window discriminator pulses in the upper traces of the pairs of recordings. The lower traces signal bladder pressure, which was monitored with a strain gauge. The records in *A* and *B* were from a unit conducting at 0·7 m/sec. The unit responded to passive distension of the bladder (*A*) but not to spontaneous contractions of the bladder (*B*). Similar results were obtained for the units whose responses are shown in *C*, *D* and in *E*, *F*. The conduction velocities of these units were 0·8 and 0·9 m/sec.

Text-fig. 8 illustrates the behaviour of three different unmyelinated afferent fibres during distension (*A*, *C*, *E*) or contraction (*B*, *D*, *F*) of the bladder. The activity of the unit in *A* and *B* is shown by window discriminator pulses on the upper traces, while pressure is recorded simultaneously using a pressure transducer connected to the lumen of a balloon placed in the bladder. In *A*, the pressure was abruptly elevated by the injection of a volume of 10 ml. saline into the bladder, with a resultant increase in the discharge of the unit. The pressure changes shown in Text-fig. 8*B* were due to spontaneous contractions of the bladder. There was no obvious correlation between the bladder contractions and the activity of the unit. Similar observations were made for the units whose activity is shown in

Text-fig. 8*C*, *D* and *E*, *F*. Injections of 7 and 9 ml. saline, respectively, caused an increase in the firing rates of the units, whereas bladder contractions did not obviously do so.

A different behaviour was noted for the myelinated ventral root afferent whose activity is shown in Text-fig. 9. The unit was judged to be myelinated on the basis of a 0·4 msec action potential duration. The action potential was recorded only with one pair of electrodes and is shown in Text-fig. 9*A*. The unit responded to an injection of 10 ml. saline into the bladder (Text-fig. 9*B*). In addition, the unit fired when the bladder contracted spontaneously, as shown in Text-fig. 9*C* and *D*. The base line bladder pressure was 3 cm water at the time of the response in Text-fig. 9*C* and 19 cm water for 9*D*.

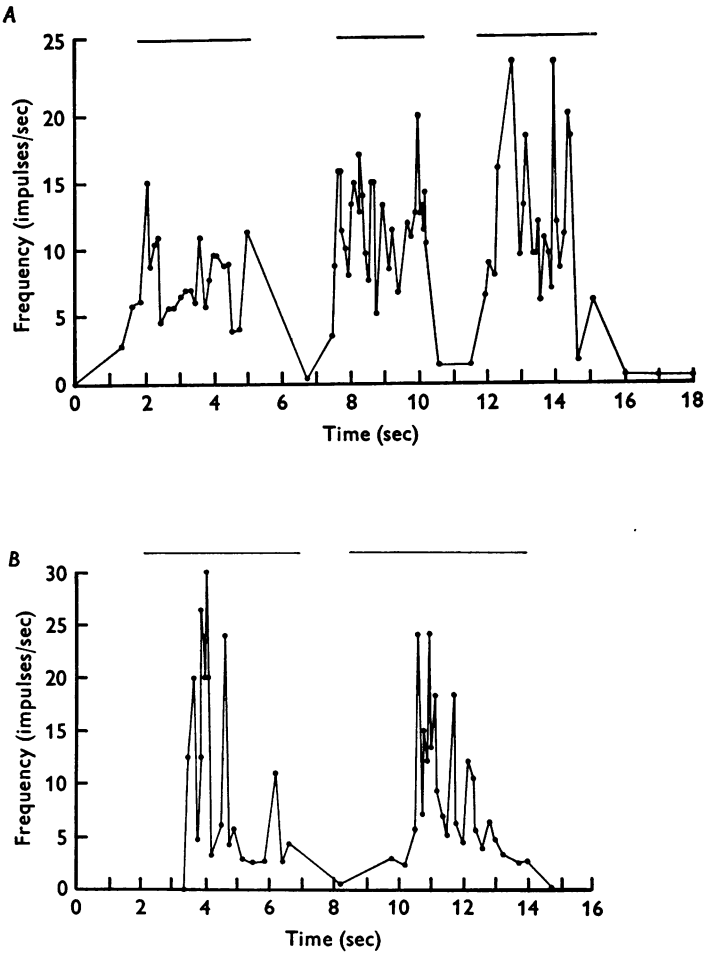


Text-fig. 9. Myelinated bladder afferent. The action potential of the unit illustrated could be recorded from just one pair of electrodes. However, since the duration of the action potential was less than 1 msec, as shown in *A*, it was assumed that the fibre was myelinated. The unit responded both to passive distension of the bladder, as shown in *B*, and during spontaneous contractions of the bladder, *C* and *D*.

Urethra. Five units with receptive fields in the urethra were studied. Four had conduction velocities appropriate to unmyelinated fibres. The other unit had a peak–peak action potential duration greater than 1 msec and so was considered to be unmyelinated. In all cases distension of the urethra was a powerful stimulus. Three units were activated by insertion of tubing into the urethra. The minimum diameter of tubing exciting these units was 2·5, 1·3 and 0·48 mm. The remaining two units were activated by a no. 8 Foley catheter. One of the units was stimulated by passing the Foley catheter into the urethra and inflating the balloon near the tip of the

catheter. The resulting activity is illustrated in Text-fig. 10*A* by an instantaneous frequency plot. Cantharidine introduced into the urethra produced a strong response in two units, and heated or cooled water had equivocal effects.

Vagina. A total of eleven units had receptive fields in the vagina or on the cervix. Conduction velocities of nine units were in the unmyelinated



Text-fig. 10. Unmyelinated afferents supplying urethra and vagina. The instantaneous frequency plot in *A* shows the responses of ventral root afferent having a conduction velocity of 0·5 m/sec to three successive inflations of a balloon at the end of a Foley catheter inserted into the urethra. The bars indicate the periods of stimulation. The responses shown in *B* were recorded from a ventral root afferent with a conduction velocity of 0·4 m/sec. The stimulus was inflation of a balloon inserted into the vagina. Two periods of stimulation are indicated by the bars.

range, while that of one unit was in the myelinated range (8 m/sec). The spike of the other unit had a peak–peak duration greater than 1 msec, and so the unit was judged to be unmyelinated.

These units, with two exceptions, required a stimulus of substantial pressure in order to be activated. Von Frey thresholds of four units examined were 100 g, 8·5 g, 500 mg and 110 mg. Of seven units examined, only two responded to heat and cantharidine. These units, which were in the same fascicle, were the units with von Frey thresholds of 500 and 110 mg. None of the units responded to cold. One unit, which did not respond to heat, cold or cantharidine, was activated by inflating a small balloon in the vagina. An instantaneous frequency plot of the resulting activity is in Text-fig. 10*B*. One unit was localized to the os cervix. It could not be activated by heat, cold, cantharidine or von Frey filaments, but was activated by pushing a glass rod against the os cervix.

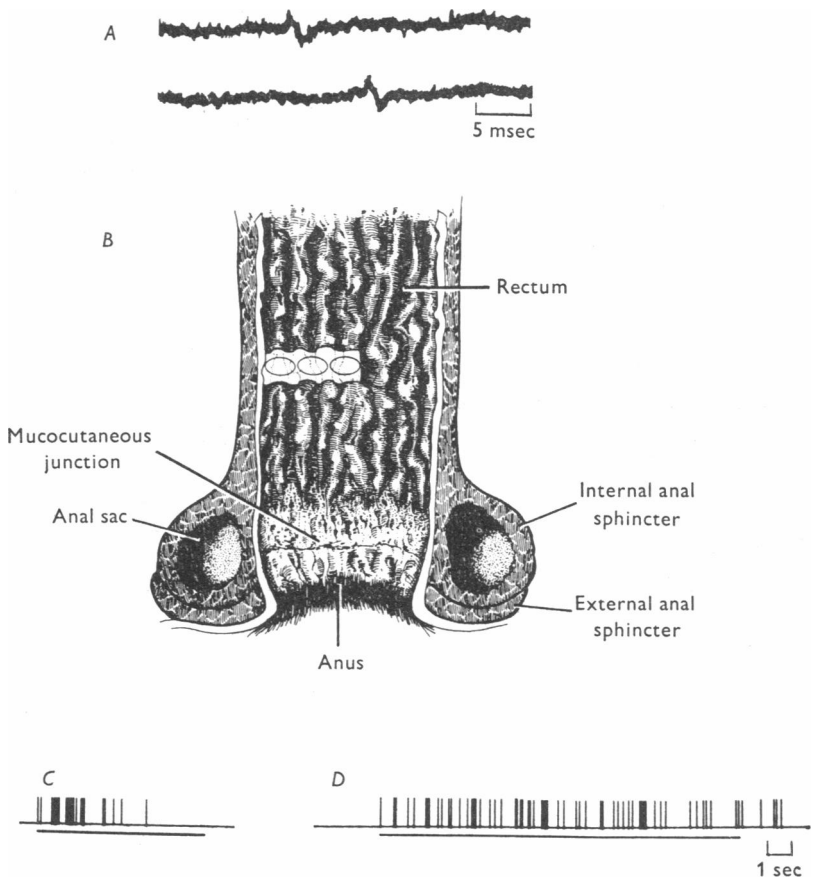
Lower bowel

As shown by Table 2, nearly half of the receptive fields found were in the lower bowel. The units could be subdivided into two categories, those which were activated by stimulation of the anal or rectal mucosa and those which responded to distension of the bowel. A limited overlap between these two categories was found.

Mucosal units. A total of twenty-eight afferents responded to stimulation of discrete areas of the anal or rectal mucosa. Of these, twenty-four had conduction velocities in the unmyelinated range, while the remaining four units were probably unmyelinated since they had action potential durations greater than 1 msec. Six of the units responded to distension of the bowel as well as to stimulation of the mucosa (cf. Paintal, 1957). Otherwise, the distinction between this category of unit and that described in the next section was clear-cut.

The stimuli which were effective in exciting mucosal units included mechanical, thermal and chemical. Mechanical stimuli which activated the afferents had to be relatively intense, including pinching the mucosa with a jeweller's forceps (Text-figs. 3*B*, 11*A* and *C*, 12*D*). No units were discharged by weak mechanical stimuli of the kind which would be interpreted as tactile when applied to the skin. Threshold determinations using von Frey filaments for mechanical stimulation were attempted for eight units with receptive fields near the anus. Only three of the afferents were activated, and these had thresholds of 3·7–12 g. The receptive fields mapped by pinching of the mucosa with jeweller's forceps usually occupied areas of 5 mm^2 or less in diameter on the side of the bowel ipsilateral to the ventral root from which the activity was recorded. Frequently, the receptive field consisted of a row of sensitive spots forming a band along the

bowel wall, as illustrated in Text-fig. 11 *B*. In two cases, the receptive field extended across the mid line to include a portion of the bowel wall contralateral to the ventral root filament. After a response was produced by pinching the mucosa, there was usually a period during which it was difficult to elicit another response. However, after a recovery period was allowed, the area regained its sensitivity to mechanical stimulation.



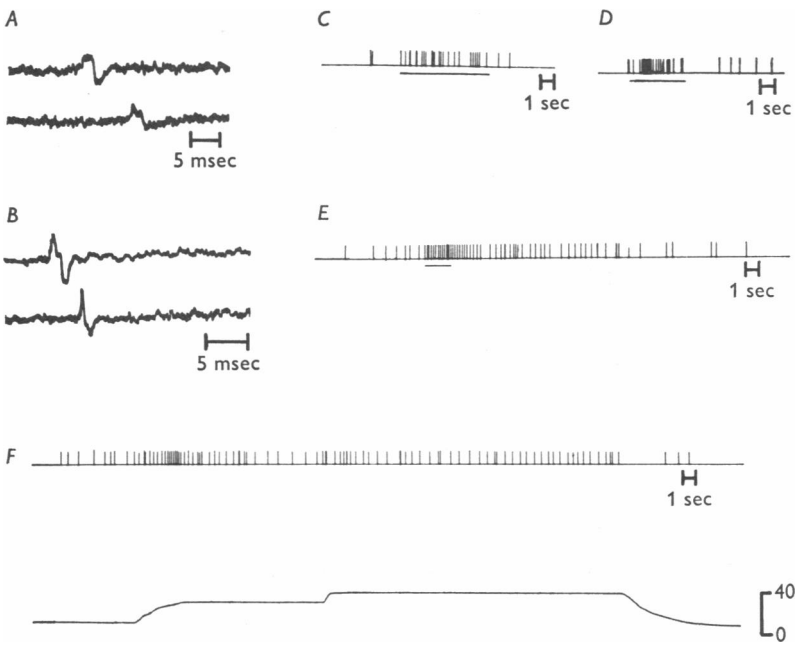
Text-fig. 11. Unmyelinated afferent supplying rectal mucosa. The action potential of a ventral root afferent conducting at 1·0 m/sec is shown in *A*. The receptive field is indicated in *B* to include a transverse strip of rectal mucosa; the ovals show the locations of three small zones of highest sensitivity to mechanical stimulation. The responses shown by window discriminator pulses in *C* was to pinching the mucosa with fine forceps. The response in *D* was to irrigation of the rectum with cold water.

Thermal stimulation consisted of the application of cooled or warmed water on to the mucosai n the area of the mechanical receptive field using a pipette. Three of the units were excited by cold water (3–8° C, measured

just before application). Two such responses are illustrated in Text-figs. 11*D* and 12*C*. Fifteen units were excited by application of water heated to 44–50° C. Of the three afferents which responded to cold water, two were also excited by hot water.

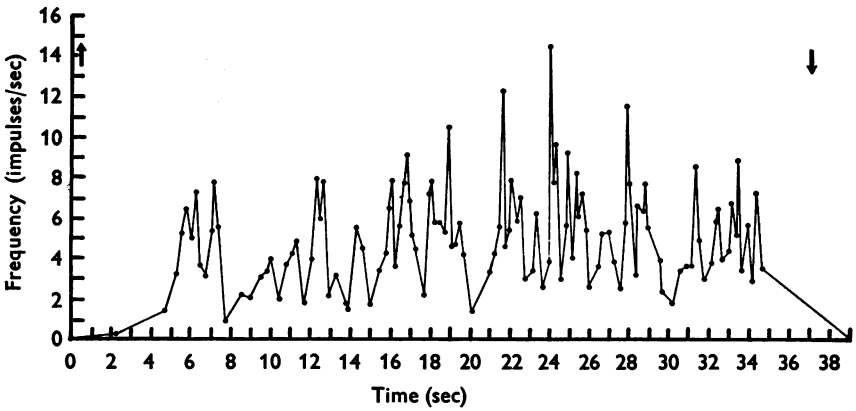
Chemical stimulation was application of a solution of cantharadin in collodion (containing camphor and other irritants). Sixteen units responded to this solution (Text-fig. 12*E*). Typically, there was a long-lasting discharge following application of the irritant. Eleven units were tested for sensitivity to 0·1 N-HCl and to 30 % NaCl, but no responses were observed.

In summary, the twenty-eight units demonstrated the following combinations of responses: pinch only (seven); pinch, heat and irritant (thirteen); pinch, cold and irritant (one); pinch, heat, cold and irritant (one). The other units were incompletely characterized.



Text-fig. 12. Units responding to mucosal stimulation or distension of bowel. The activity of two units is shown. The action potential in *A* was recorded from a ventral root afferent with a conduction velocity of 0·7 m/sec. This unit was activated by irrigation of the lower bowel with cold water, *C*, stimulation of the mucosa by pinch, *D*, or application of the irritant chemical, cantharidine, to the mucosa, *E*. The action potential of another ventral root afferent supplying the lower bowel is shown in *B*. This fibre conducted at 2·0 m/sec. It responded to distension of the lower bowel by inflation of a balloon; this response is shown in the upper trace in *F*; the lower trace is a recording taken simultaneously of the pressure within the balloon.

Distension-sensitive units. A total of seventeen afferents were found which responded to distension of the bowel. Of these, fourteen were shown to have conduction velocities in the unmyelinated range, while another was probably unmyelinated because its action potential had a long duration. Two afferents were myelinated.



Text-fig. 13. Distension sensitive unit supplying colon. The response of a ventral root afferent fibre with a conduction velocity of 0·6 m/sec to inflation of a balloon placed in the lower colon is shown by the instantaneous frequency plot. Inflation began at the first arrow and terminated at the second arrow.

The bowel was distended by inflation of a latex balloon with warmed saline, while pressure was monitored using a pressure transducer. The afferents generally displayed little or no spontaneous activity before or after distension, and their thresholds to distension were usually between 15 and 35 cm water. The responses were slowly adapting, although there was sometimes an initial dynamic response. Examples are shown in Text-figs. 12*F* and 13. The afferents could also generally be excited by pressure applied to a restricted region of the wall of the bowel or of deep tissues in the perianal region ipsilateral to the ventral root. However, with the exception of the afferents mentioned in the previous section, the units tested did not respond to stimuli applied to the mucosa, whether the forms of stimulation were pinching, thermal changes or application of chemical irritants. Of the units studied, four were in the colon, eight in the rectum, and three in the anal canal.

DISCUSSION

The companion study to the present paper demonstrated that 29% of the axons in the S3 and Ca 1 roots of the cat are unmyelinated and that approximately half of these unmyelinated axons arise from dorsal root

ganglion cells (Applebaum *et al.* 1975). These findings suggest that a significant fraction of the S3 and Ca 1 ventral root axons are sensory. It should be remembered that the morphological data may not provide an exact estimate of the number of ganglion cells giving rise to afferent ventral root axons, at least in the S2, S3 and Ca 1 cat ventral roots, because there is electrophysiological evidence that 11–23% of the fibres branch within the ventral root. However, it is not clear where the branching occurs and so for the present we cannot modify our ventral root counts.

To demonstrate a sensory function, the activity of single axons was recorded in filaments of the S3 and Ca 1 ventral roots. Receptive fields for these axons were demonstrated by appropriate stimulation at the periphery. Based on conduction velocities, ninety-three unmyelinated and fourteen myelinated axons were studied. In addition, receptive fields were demonstrated for thirteen other axons whose conduction velocity could not be determined, but whose peak–peak spike duration suggested that they were unmyelinated.

In the S3 and Ca 1 segments, two-thirds of the receptive fields of ventral root unmyelinated axons were located in the viscera and one third were found in some somatic tissues. However, all of the twelve units which were recorded from the chronically sectioned S2 ventral root in one animal had cutaneous receptive fields. This result might suggest that cutaneous receptive fields are more common at the level of the spinal enlargements, but more studies will be necessary before this suggestion can be accepted. In this regard, behavioural tests have not shown residual cutaneous or proprioceptive sensibility in limbs or other parts of the body which are deafferented by dorsal rhizotomy (Knapp, Taub & Berman, 1963; Taub, Goldsbery & Taub, 1975). Nevertheless, the finding of significant numbers of somatic sensory fibres in the ventral roots should be remembered when such studies are interpreted.

The cutaneous receptive fields demonstrated in the present experiments were similar to those described for unmyelinated afferents recorded from peripheral nerves (Iggo, 1960; Bessou & Perl, 1969). For the eighteen units activated with von Frey filaments, seventeen had high thresholds. Furthermore, three of the seventeen high threshold units responded both to noxious mechanical and thermal stimuli and were thus polymodal nociceptors (Bessou & Perl, 1969). We can, therefore, conclude that most of the unmyelinated ventral root afferents studied having cutaneous receptive fields are involved in nociception. Although the location of the receptive fields and the types of stimuli required to activate the ventral root afferents are not different from those axons of similar sizes in peripheral nerve, the fact that such a large proportion of the cutaneous ventral root fibres are high threshold is of some interest. One possibility is that we are misled because

of a small sample. Another possibility, however, is that a higher proportion of ventral root afferents are concerned with nociception than is the case for peripheral nerve (Bessou & Perl, 1969). It will be important to determine if the proportion of nociceptors is the same or different in the dorsal roots of these same segments. It is interesting that myelinated ventral root afferents with low threshold cutaneous receptive fields have been reported (Kato & Hirata, 1968; Ryall & Piercey, 1970; Kato & Tanji, 1971).

Some of the somatic units that we studied had deep receptive fields. Several unmyelinated fibres discharged in a slowly adapting fashion when joints of the tail were bent. The stimuli used were strong, but it is not clear whether or not the stimuli were noxious. If not, proprioceptive information may reach the central nervous system over unmyelinated afferents. We did not determine whether these afferents innervated muscle or joints. Others have reported myelinated ventral root afferents from muscle (Dimsdale & Kemp, 1966; Kato & Hirata, 1968; Kato & Tanji, 1971) and joints (Kato & Tanji, 1971). In no case did nociceptive cutaneous stimuli activate these units.

The units supplying the bladder and urethra were comparable to the afferents from these structures described by others (Talaat, 1937; Iggo, 1955; Todd, 1964; Winter, 1971). Myelinated ventral root afferents from the bladder were reported by Ryall & Piercey (1970). One difference between the unmyelinated and myelinated afferents in our sample was that the former did not discharge during spontaneous bladder contractions, whereas the latter did. Furthermore, the thresholds for the unmyelinated afferents were higher than for the myelinated afferents in our study, but we cannot say whether this means that the unmyelinated ventral root bladder afferents are nociceptors.

The activity recorded from afferents supplying the lower bowel was similar to that reported by other workers (Iggo, 1957; Paintal, 1957). In our study one interesting finding was that the majority of mucosal units were similar to cutaneous polymodal nociceptors (Bessou & Perl, 1969). However, as Paintal pointed out (1957), the response to various types of mechanical and chemical stimuli could be secondary to reflex contractions set up in the muscularis mucosae. Further study will be necessary to determine the role of the ventral root afferents in nociception from the gut.

The above data would seem to indicate that the ventral root contains a large number of sensory fibres that enter the central nervous system. These may explain the observations that stimulation of ventral roots produces pain both in animals (Magendie, 1822*b*; Bernard, 1858) and in humans (Frykholm, 1951; Frykholm *et al.* 1953; White & Sweet, 1955). Furthermore, the persistence of pain after dorsal rhizotomy might be related to these fibres. In this regard, Coggeshall *et al.* (1975) showed that every

ventral root in the human contains large numbers of unmyelinated fibres and suggested that many of these fibres are sensory. However, many investigators would not accept this reasoning. We quote Cranefield's (1974) summary of other ideas put forward to explain these phenomena: The possible explanations (for the production of pain by ventral root stimulation)...include: (1) direct excitation of sensory fibres that start toward the cord in the ventral root and loop back into the dorsal root; (2) direct excitation of sensory fibres that arise in the accessory structures of the ventral root and reach the cord via the dorsal root; (3) direct excitation of sensory fibres that actually reach the cord via the ventral root (this explanation is incompatible with abolition of the pain by dorsal root section); (4) direct excitation of sympathetic fibres; (5) ephaptic excitation of sensory fibres in the mixed spinal nerve by the action potentials of motor fibres; (6) ephaptic excitation of sensory fibres by the action potential of the skeletal muscle itself; (7) muscular contraction causing a strong synchronous burst of impulses from tendon and muscle receptors, that might sometimes appear as pain or that might ephaptically excite pain fibres; (8) a burst of sensory impulses resulting from the "resetting" of the muscle spindles in the fashion discovered by Leksell, perhaps sometimes appearing as pain or ephaptically exciting pain fibres; (9) other mechanisms by which pain fibres are stimulated within the muscle.'

Explanations (5)–(9), which involve ephaptic stimulation of sensory fibres or activation of afferents by muscular contractions clearly do not apply in our study. The animals were paralysed and so lacked muscular activity, and electrical stimuli were not used, so there were no synchronous volleys to produce ephaptic interactions. In addition, sensory units could be found in chronically sectioned ventral roots where there could be no motor activity at all. The chronic ventral root section also rules out explanation (4) because the sympathetic fibres would not conduct antidromically after 3 weeks' degeneration. Explanation (2), the excitation of accessory structures in the ventral root is not correct because the receptive fields we found were not located in the vicinity of the ventral root, but were located in pelvic viscera or peripheral somatic tissue.

Perhaps the best evidence in favour of explanation (1), that sensory fibres start towards the cord in the ventral root and then loop back into the dorsal root, are observations by Magendie (1822*b*) and Claude Bernard (1858), who noted that stimulation of the distal end of a cut ventral root caused 'pain' in experimental animals and that section of the dorsal root abolished the pain. Frykholm (1951) and Frykholm *et al.* (1953) extended this work to humans by showing that stimulation of irritated ventral roots caused pain and that the pain was abolished when the dorsal root was cut or anaesthetized. However, our anatomical evidence is not consistent with

explanation (1). For example, if axons loop as Cranefield (1974) suggests, then a section of the ventral root would separate from their cell bodies all axons in the proximal stump and half the axons in the distal stump. (The other half of the axons in the distal stump are the ones that are still connected to their cell bodies in the dorsal root ganglion.) Since axons separated from their cell bodies die, the counts should indicate that all sensory axons from the proximal stump and half the sensory axons from the distal stump are gone. Our data (Applebaum *et al.* 1975) for the S3 and Ca 1 cat ventral roots seem to show, however, that although the afferent axons are gone in the proximal stump, all are *present* in the distal stump. It must be admitted that the presence of unmyelinated efferent fibres complicate the counts in the S3 and Ca 1 roots, but in roots L7 and S1 there are very few, if any, unmyelinated efferents, and the figures seem to indicate that all sensory axons disappear in the proximal stump and remain in the distal stump (Coggeshall *et al.* 1974). It is also possible that sensory axons carrying information centrifugally in the ventral root could approach the root via peripheral nerves from other body segments and then join the ventral root in question by such gross connexions as were recently illustrated by Jacob & Weddell (1975). We have not seen such connexions, however. Furthermore, we followed two S1 ventral root fascicles to the spinal cord and found that the unmyelinated fibres were present in the same approximate distributions and numbers at the junction of the root with the cord as more distally in the root (R. E. Coggeshall, J. D. Coulter & W. D. Willis, unpublished observations). Thus, if there were sensory fibres that either looped in the ventral root or passed to the ventral root from other roots, they would presumably first have to go into the spinal cord and then travel back into the ventral root, a possibility that seems unlikely. Finally, preliminary observations after cutting the dorsal root and injecting horseradish peroxidase into the spinal cord indicate that some dorsal root ganglion cells are labelled (Maynard, Leonard, Coulter, Coggeshall & Willis, 1975), a finding that implies that fibres in the ventral root enter the spinal cord and synapse there. For these reasons, we feel that the bulk of the available evidence is against the supposition that the sensory axons in the ventral root carry information centrifugally and do not enter the spinal cord. Thus, we are left with explanation (3), that the ventral root sensory fibres enter the spinal cord through the ventral root.

If it be accepted that the ventral root sensory axons pass into the spinal cord via the ventral root, then the sensation of pain that comes when the ventral root is stimulated would presumably come from activation of these fibres. However, the cessation of ventral root pain when the dorsal root was interrupted could not, in this case, be explained by the looping of the ventral root fibres into the dorsal root. A possible explanation might be

that dorsal root sensory axons are necessary to maintain a level of excitability that allows ventral root sensory impulses to activate cells in long ascending pain pathways (e.g. Frykholm *et al.* 1953). Alternatively, it is possible that the ventral root axons arise from trifurcate dorsal root ganglion cells, cells with (1) a peripheral process, (2) a central process in the dorsal root and (3) a central process in the ventral root. In this case, an interaction of impulses in both central processes might be necessary to produce pain. A trifurcate dorsal root ganglion cell with myelinated processes has been discovered (Loeb, 1975). Studies demonstrating the central projections and physiological actions of the ventral root afferents will be necessary to resolve this issue.

The present study demonstrates there is a significant number of unmyelinated sensory fibres in the ventral root and confirms the presence of myelinated sensory fibres in these same roots. The receptive fields of the unmyelinated ventral root afferents do not seem to differ from receptive fields of unmyelinated fibres in peripheral nerves, but at the S3 and Ca 1 levels there does seem to be (1) a relatively high proportion of visceral afferents, and (2) a relatively high proportion of cutaneous nociceptive fibres. These data, combined with the observation that 15% of the axons in these roots from dorsal root ganglion cells (Applebaum *et al.* 1975), imply that there is an important sensory component in the ventral root. Furthermore, nearly 30% of the fibres in the L7 and S1 ventral roots are probably sensory (Coggeshall *et al.* 1974). If this is true, then the Law of Bell and Magendie is not an accurate description of the organization of ventral roots in the cat.

The authors thank M. L. Applebaum for her assistance in electron microscopy and Gail Silver for her technical help. This work was supported by Program Project Grant NS 11255, Research Grant NS 10161, and Training Grant NS 05743 from the National Institutes of Health, U.S. Public Health Service, and a grant from the Moody Foundation of Galveston.

REFERENCES

APPLEBAUM, M. L., CLIFTON, G. L., COGGESHALL, R. E., COULTER, J. D., VANCE, W. H. & WILLIS, W. D. (1976). Unmyelinated fibres in the sacral 3 and caudal 1 ventral roots of the cat. *J. Physiol.* **256**, 557–572.

BELL, C. (1811). Idea of a new anatomy of the brain. Reprinted in *The Way In and the Way Out*, ed. CRANEFIELD, P. F. (1974). London: Strahan and Preston.

BERNARD, C. (1858). *Leçons sur la Physiologie et la Pathologie du Système Nerveux*, tome 1, pp. 20–112. Paris: Baillière et fils.

BESSOU, P. & PERL, E. R. (1969). Response of cutaneous sensory units with unmyelinated fibers to noxious stimuli. *J. Neurophysiol.* **32**, 1025–1043.

CLIFTON, G. L., VANCE, W. H., APPLEBAUM, M. L., COGGESHALL, R. E. & WILLIS, W. D. (1974). Responses of unmyelinated afferents in the mammalian ventral root. *Brain Res.* **82**, 163–167.

COGGESHALL, R. E., APPLEBAUM, M. L., FRAZEN, M., STUBBS, T. B. & SYKES, M. T. (1975). Unmyelinated axons in human ventral roots, a possible explanation for the failure of dorsal rhizotomy to relieve pain. *Brain* **98**, 157–166.

COGGESHALL, R. E., CLIFTON, G. L., VANCE, W. H. & APPLEBAUM, M. L. (1975). Unmyelinated sensory fibers in the ventral root. *Anat. Rec.* **181**, 334.

COGGESHALL, R. E., COULTER, J. D. & WILLIS, W. D. (1974). Unmyelinated axons in the ventral roots of the cat lumbosacral enlargement. *J. comp. Neurol.* **153**, 39–58.

CRANEFIELD, P. F. (1974). *The Way In and the Way Out: Francois Magendie, Charles Bell and The Roots of the Spinal Nerves*. New York: Futura Publishing Co.

DAVIS, L. & POLLOCK, L..J. (1930). The peripheral pathway for painful sensations. *Archs Neurol. Psychiat., Chicago* **24**, 883–893.

DIMSDALE, J. A. & KEMP, J. M. (1966). Afferent fibres in ventral roots in the rat. *J. Physiol.* **187**, 25–26*P*.

FRYKHOLM, R. (1951). Cervical root compression resulting from disc degeneration and root-sleeve fibrosis. A clinical investigation. *Acta chir. scand.* (suppl.) 160.

FRYKHOLM, R., HYDE, J., NORLEN, G. & SKOGLUND, C. R. (1953). On pain sensations produced by stimulation of ventral roots in man. *Acta physiol. scand.* **29**, suppl. 106, 455–469.

GASSER, H. S. (1950). Unmedullated fibers originating in dorsal root ganglia. *J. gen. Physiol.* **33**, 651–690.

IGGO, A. (1955). Tension receptors in the stomach and the urinary bladder. *J. Physiol.* **128**, 593–607.

IGGO, A. (1957). Gastro-intestinal tension receptors with unmyelinated afferent fibres in the vagus of the cat. *Q. Jl exp. Physiol.* **42**, 130–143.

IGGO, A. (1960). Cutaneous mechanoreceptors with afferent C fibres. *J. Physiol.* **152**, 337–353.

JACOB, M. & WEDDELL, G. (1975). Neural intersegmental connection in the spinal root and ganglion region of the rat. *J. comp. Neurol.* **161**, 115–124.

KATO, M. & HIRATA, Y. (1968). Sensory neurons in the spinal ventral roots of the cat. *Brain Res.* **7**, 479–482.

KATO, M. & TANJI, J. (1971). Physiological properties of sensory fibers in the spinal ventral roots in the cat. *Jap. J. Physiol.* **21**, 71–77.

KIDD, L. J. (1911). Afferent fibres in ventral spinal roots. *Br. med. J.* **2**, 359–360.

KNAPP, H. D., TAUB, E. & BERMAN, A. J. (1963). Movements in monkeys with deafferented forelimbs. *Expl Neurol.* **7**, 305–315.

LEHMANN, W. (1924). Über die sensiblen Fasern der vorderen Wurzeln. *Klin. Wschr.* **3**, 1895–1898.

LOEB, G. E. (1975). Ventral root projections of myelinated dorsal root ganglion cells in the cat. *Neurosci. Abstracts*, p. 142 (Society for Neurosciences, 5th Annual Meeting, New York).

LOESER, J. D. (1974). Dorsal rhizotomy: Indications and results. *Adv. Neurol.* **4**, 615–619.

MAGENDIE, F. (1822*a*). Expériences sur les fonctions des racines des nerfs rachidiens. *J. Physiol. exp. Path.* **2**, 276–279. Reprinted in *The Way In and the Way Out*, ed. CRANEFIELD, P. F. (1974). London: Strahan and Preston.

MAGENDIE, F. (1822*b*). Expériences sur les fonctions des racines des nerfs qui naissent de la moelle épiniere. *J. Physiol. exp. Path.* **2**, 366–371. Reprinted in *The Way In and the Way Out*, ed. CRANEFIELD, P. F. (1974). London: Strahan and Preston.

MAYNARD, C. W., LEONARD, R. B., COULTER, J. D., COGGESHALL, R. E. & WILLIS, W. D. (1975). Cells of origin of ventral root afferents. *Neurosci. Abstracts*, p. 141 (Society for Neurosciences, 5th Annual Meeting, New York).

MIKELADZE, A. L. (1965). Endings of afferent nerve fibers in lumbosacral region of spinal cord. *Fedn Proc.* **26**, T211–T216. Translated from the Russian *Arkh. Anat. Gistol. Embriol.* **48**, 3–13.

ONOFRIO, B. M. (1974). Rhizotomy: What is its place in the treatment of pain? *Adv. Neurol.* **4**, 621–623.

PAINTAL, A. S. (1953). The conduction velocities of respiratory and cardiovascular afferent fibres in the vagus nerve. *J. Physiol.* **121**, 341–359.

PAINTAL, A. S. (1957). Responses from mucosal mechanoreceptors in the small intestine of the cat. *J. Physiol.* **139**, 353–368.

PAINTAL, A. S. (1967). A comparison of the nerve impulses of mammalian non-medullated nerve fibres with those of the smallest diameter medullated fibres. *J. Physiol.* **193**, 523–533.

RYALL, R. W. & PIERCEY, M. F. (1970). Visceral afferent and efferent fibers in sacral ventral roots in cats. *Brain Res.* **23**, 57–65.

SHAW, R. C. (1933). Sympathetic system and pain phenomena. *Archs Surg., Chicago* **27**, 1072–1080.

SHERRINGTON, C. S. (1894). On the anatomical constitution of nerves of skeletal muscles, with remarks on recurrent fibres in the ventral spinal nerve root. *J. Physiol.* **17**, 211–258.

STEADMAN, R. M. (1968). A feedback controlled thermal stimulator. *Proc. Ann. Conf. Engr. Med. Biol.* p. 18.2.

TALAAT, M. (1937). Afferent impulses in the nerves supplying the urinary bladder. *J. Physiol.* **89**, 1–13.

TAUB, E., GOLDBERG, I. A. & TAUB, P. (1975). Deafferentation in monkeys: Pointing at a target without visual feedback. *Expl Neurol.* **46**, 178–186.

TODD, J. K. (1964). Afferent impulses in the pudendal nerves of the cat. *Q. Jl exp. Physiol.* **49**, 258–267.

VANCE, W. H., CLIFTON, G. L., COGGESHALL, R. E. & WILLIS, W. D. (1975). Receptive field properties of unmyelinated ventral root afferents. *Fedn Proc.* **34**, 388.

WARTENBERG, R. (1928). Klinischen Studien zur Frage der Geltung des Bell-Magendieschen Gesetzes. *Z. ges. Neurol. Psychiat.* **113**, 518–603.

WEBBER, R. H. & WEMETT, A. (1966). Distribution of fibers from nerve cell bodies in ventral roots of spinal nerves. *Acta anat.* **65**, 579–583.

WHITE, J. C. & SWEET, W. H. (1955). *Pain: Its Mechanisms and Neurosurgical Control.* Springfield: Thomas.

WINDLE, W. F. (1931). Neurons of the sensory type in the ventral roots of man and of other animals. *Archs Neurol. Psychiat., Chicago* **26**, 791–800.

WINTER, D. L. (1971). Receptor characteristics and conduction velocities in bladder afferents. *Jnl psychiat. Res.* **8**, 225–235.

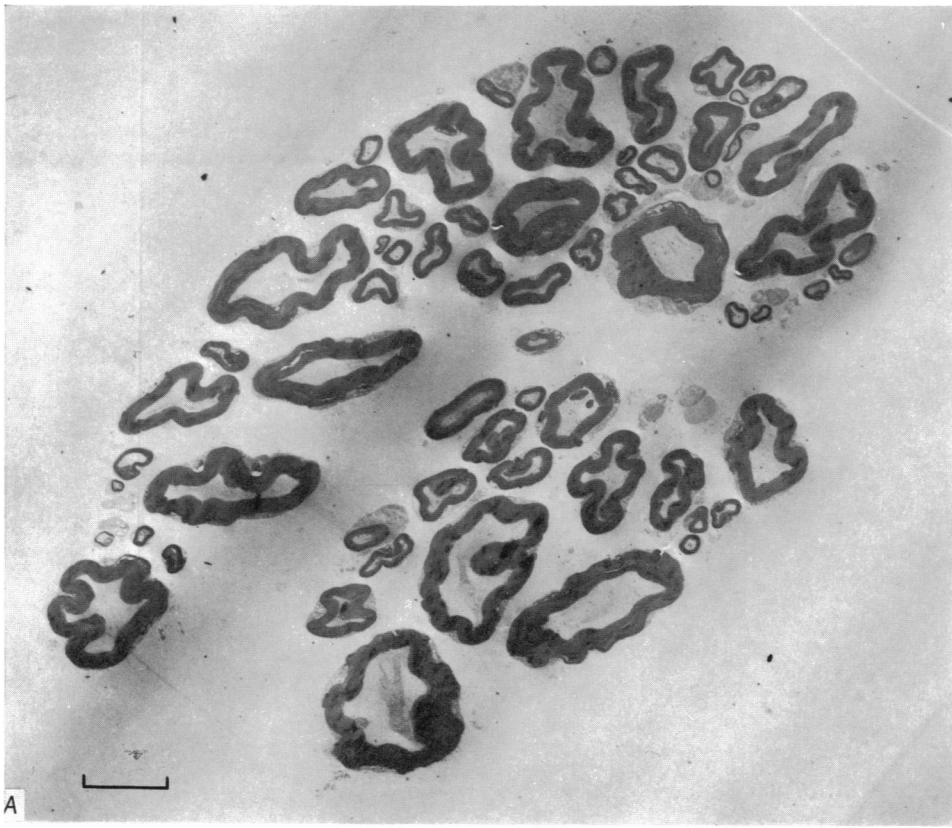
EXPLANATION OF PLATES

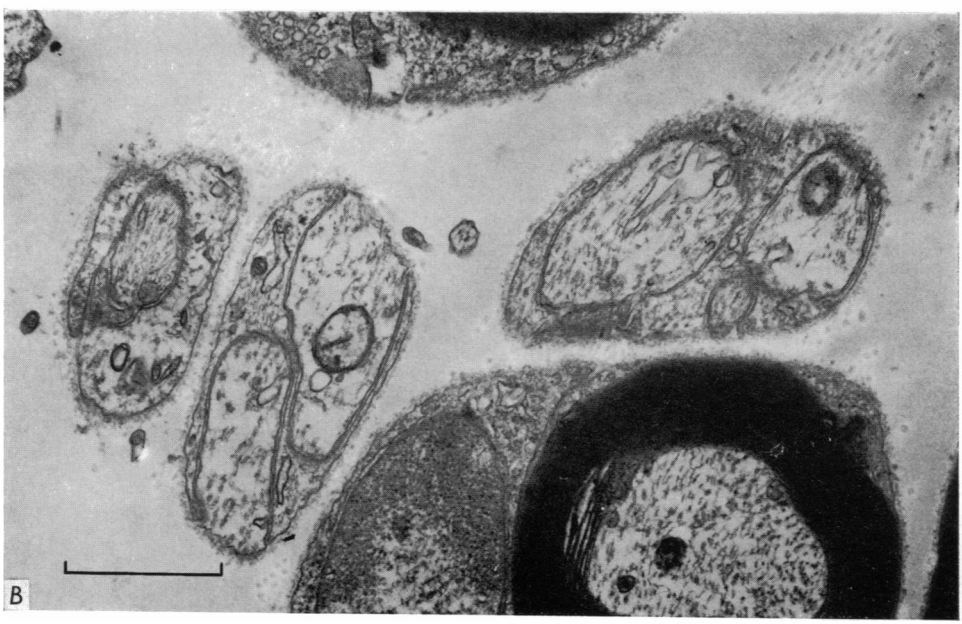
PLATE 1

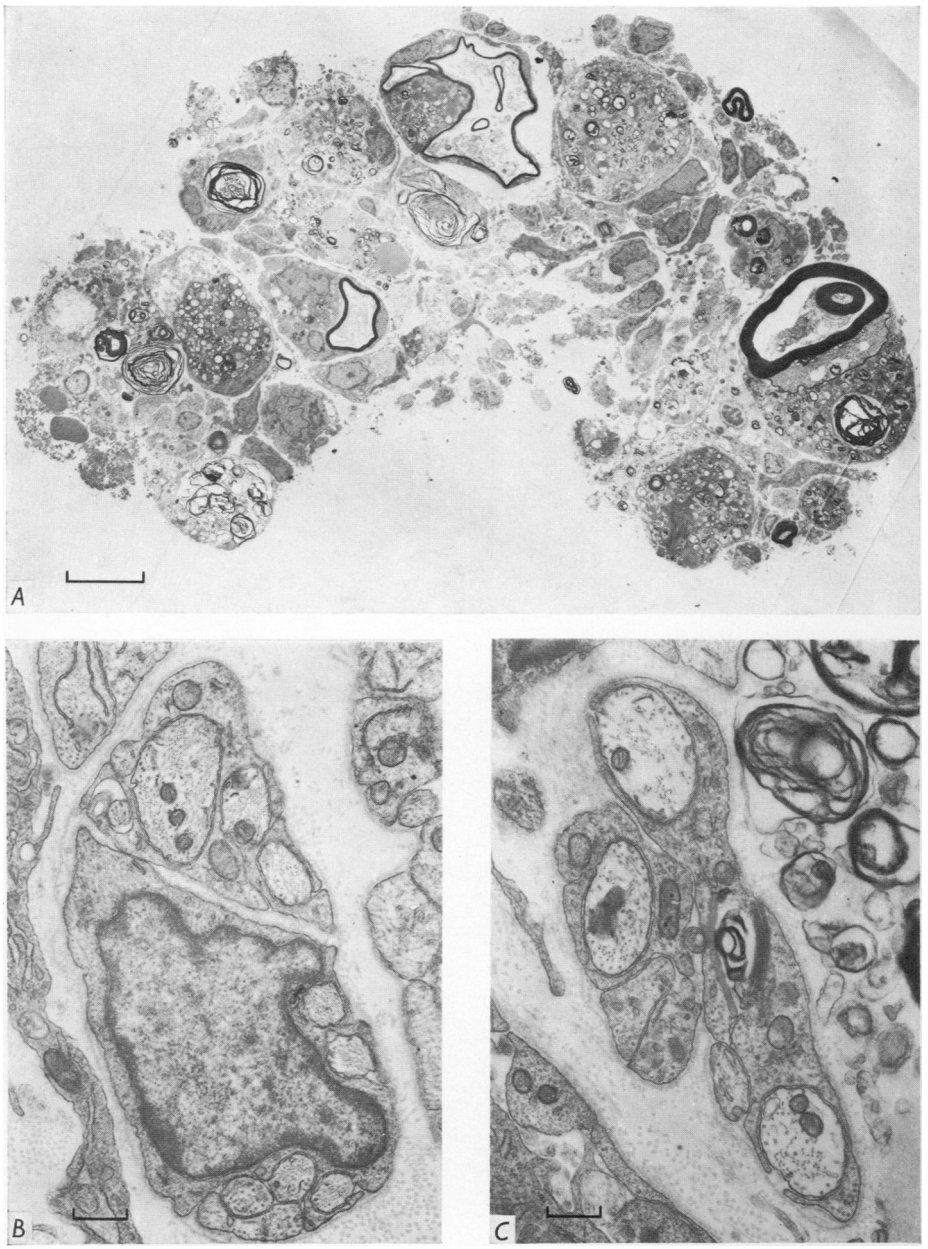
A, this is an electron micrograph of a ventral root fascicle. The myelinated fibres have become separated somewhat either from the dissection or during their tenure in mineral oil. The recording from this filament is illustrated in Text-fig. 3. Calibration bar indicates 10 μm. *B*, this picture illustrates three small Remak bundles from the above filament. The unmyelinated axons are not significantly different from the unmyelinated axons in normal roots. Calibration bar indicates 1 μm.

PLATE 2

A, this is an electron micrograph of a filament of a ventral root that has been sectioned proximally 3 weeks before. Note the extensive degeneration of the myelinated fibres. Calibration bar indicates 10 μm. *B* and *C*, these are electron micrographs of Remak bundles from the above filament. Note the normal appearance of the unmyelinated axons. Calibration bar indicates 0·5 μm.


A


B


A
B
C